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Grandmothering in *Galago senegalensis braccatus* (Senegal Galago)

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Abstract: This is the first detailed analysis of allonursing in a galago, a relatively nongregarious African strepsirrhine. Existing data on allonursing in galagos are scarce due to the difficulties of observing wild infant behavior in nocturnal species that frequently raise young in nests, and to the rarity of colonies with multiple co-housed lactating females. We determined the kin relations between subjects, quantified the prevalence of allonursing, searched for opportunities for allonursing in which it did not occur, and qualitatively compared growth rates of infants that were and were not allonursed. Focal adult and infant observations of *Galago senegalensis braccatus* were made in the Arizona State University colony between 1976 and 1990. The colony contained two matrilines caged separately because unrelated adult females are extremely aggressive to each other. The groups ranged from two to seven individuals. The availability of simultaneously lactating females within one group varied over time. Allonursing occurred in both matrilines and in a total of four infants (two males, two females). For one male, this represented a single event with an older sister. More prevalent allonursing occurred in both matrilines with the remaining male and two females, each allonursed by maternal grandmothers in 21% (n=104), 25% (n=52), and 27% (n=92) of their observed nursing bouts, respectively. Qualitative comparisons do not suggest that allonursed and non-allonursed infants grow at different rates. Intriguingly, maternal grandmothers frequently allonursed grandchildren, but adult daughters rarely reciprocated by allonursing younger siblings. Overall, our findings suggest that grandmothering may be a form of kin selection in this species and that it may enable older females, some of which had lost a neonate, to increase their reproductive success.

Key words: lesser bushbaby, galago, *Galago senegalensis*, grandmothers, nursing, alloparental care, maternal care, captivity

Résumé: *Il s'agit de la première analyse détaillée d'allaitement mixte chez un galago, un strepsirrhinien Africain relativement peu gregaire. Les données existantes sur l'allaitement mixte chez les galagos sont rares en raison des difficultés d'observer le comportement infantile chez les espèces sauvages nocturnes qui élèvent fréquemment les nourrissons dans des nids, et de la rareté des colonies avec plusieurs femelles co-logées en période de lactation en même temps. Des observations focales sur les adultes et des nourrissons* Galago senegalensis braccatus *ont été réalises sur la colonie hébergée a l'Université d'état de l'Arizona entre 1976 et 1990. Nous avons déterminé les relations de parenté entre les individus, quantifier la prévalence de l'allaitement mixte, recherchez des opportunités pendant lesquels l'allaitement mixte n'a pas eu lieu, et comparez les taux de croissance des nourrissons entre ceux qui ont été allaité mixtement et ceux qui ne l'ont pas été. La colonie contenait deux matrilignages qui étaient hébergés dans des cages séparés à cause du comportement extrêmement agressifs entre les femelles de différentes matrilignage. Les groupes étaient composés de deux à sept individus. La disponibilité des femelles qui allaitent en même temps dans un groupe a aussi varié avec le temps. L'allaitement mixte a eu lieu dans les deux lignées maternelles. Quatre nourrissons (2 mâles, 2 femelles) on ainsi été observer en allaitement mixte. Pour l'un des mâles, cela a représenté un événement unique avec une sœur aînée. Il y a eut plus d'allaitement mixte dans les deux lignées maternelles avec le mâle et deux femelles nourrissons restants, chacun ayant été allaiter par les grands-mères maternelles dans 21% (n = 104), 25% (n = 52), et 27% (n = 92) des cas respectifs. Des comparaisons qualitatives ne suggèrent pas que les nourrissons en allaitement mixte et ceux en allaitement normal croît à des taux différents. Curieusement, les grands-mères maternelles ont souvent allaité leurs petits-enfants, mais les femelles adultes ont rarement réciproqué en allaitant leur jeunes frères ou sœurs. Dans l'ensemble, nos résultats suggèrent que l'importance de la grand-mère peut être une forme de sélection de parentèle chez cette espèce et qu'elle peut permettre à des femelles plus âgées, dont certains ont perdu un nouveau-né, d'augmenter leur succès reproducteurs.*

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INTRODUCTION

Kin selection is thought to have been a driving force in the evolution of primate sociality (Hamilton, 1964; Chapais & Berman, 2004). By behaving in ways that benefit kin, an individual can help perpetuate his/her genes in the population indirectly, rather than directly by raising additional offspring (Hamilton, 1964). Such selection is likely to have been crucial during the evolution of the diversity of kin-based social systems seen today in the primate order (Chapais & Berman, 2004).

An extreme form of kin selection is cooperative breeding with kin (Chapais & Berman, 2004; Kappeler & van Schaik, 2006; Hrdy, 2005, 2009). In these breeding systems related individuals alloparent (help rear) offspring that are not their own (Chapais & Berman, 2004; Kappeler & van Schaik, 2006; Hrdy, 2009). Though *elements* of cooperative breeding (i.e., holding another's infant) are common among primates (Chapais & Berman, 2004; Kappeler & van Schaik, 2006), "full-fledged" cooperative breeding, which entails both alloparental care and extensive provisioning of young (including, but not limited to allomaternal nursing) and mothers, is rare in primates. More modest forms of it (alloparental care plus at least minimal provisioning) occur more commonly than generally realized, characterizing perhaps 20% of primates (Hrdy 2009). Broadly defined as alloparental care plus some degree of alloparental provisioning, cooperative breeding has evolved multiple times. It evolved convergently in humans, the callitrichines, some cercopithecine monkeys (patas, talapoin and some quenons), ruffed lemurs and mouse lemurs, and possibly spectral tarsiers and ringtail lemurs (Pereira & Izard, 1989; Morland, 1990; Gould, 1992; Snowdon, 1996; Chism, 2000; Gursky, 2000; Eberle & Kappeler, 2006; Vasey, 2007; Sear & Mace, 2008). Among galagos, such alloparental activities would be expected to be seen in females; males are not substantially involved in care of infants (Wright, 1990; Nekaris & Bearder, 2007). In this paper, we concentrate on the most direct form of allocare that a female might provide: allonursing (for brevity, but etymologically more correctly, 'allomaternal nursing').

Presented here is the first detailed analysis of allonursing in galagos. Existing data on alloparenting in galagos is scarce, likely due to the difficulties of observing wild infant behavior in nocturnal species that raise their young in nests, tree holes, or tangles of vegetation (Bearder, 1987), and because captive colonies with multiple, co-housed, lactating females are rare. The literature does suggest, however, that at least some galago species may engage in some cooperative breeding behavior. Captive *Otolemur crassicaudatus* have been observed to retrieve and allonurse other females' young (Welker & Schaferwitt, 1988), and wild females may groom, stay near ("babysit"), or lead each other's young (Clark, 1985). Female *Galago moholi* have been observed raising offspring in the same nest (Bearder, 1987) and allonursing in captivity (Doyle *et al.*, 1969). Intriguingly, those observations do not seem to indicate that all galagos provide allocare. *Galagoides demidovii* mothers separate themselves from their sleeping groups for the first 1-2 weeks of their infants' lives (Charles-Dominique, 1977). *Galagoides cocos (*formerly '*zanzibaricus*'; following Grubb *et al.*, 2003) mothers sleep alone for the first three weeks of their infants' lives, occasionally joined by an adult male, but not an adult female (Harcourt, 1986). Such separations would limit the opportunities for allocare during that time. Here, we present the first data on *G. senegalensis braccatus,* a small-bodied, nocturnal solitary forager that subsists on a diet of gums and insects (Kingdon, 1971; Nash & Whitten, 1989). Females gestate their young for approximately 142 days, giving birth to 1-2 infants which are parked in a nest and transported orally (Nash, 1993). Weaning occurs at about 10 weeks of age (Nash, 1993). In contrast to a high frequency of twinning in *Galago moholi* (formerly included within *G. senegalensis* (Groves, 2001)), the prevalence of twining in this colony of *G. senegalensis* has been only 8% in 62 births (Izard & Nash, 1988).

The nocturnal, nongregarious strepsirrhine primates are interesting taxa in which to investigate cooperative breeding behavior because their relatively solitary lifestyle has been argued to be similar to that of the last common ancestor of primates (Müller & Thalmann, 2000). These species forage alone at night, but maintain structured, though dispersed, social networks, communicating with individuals that are distant in space via auditory cues (vocalizations), and with individuals which are distant in time via olfactory cues (scent marks) (Müller & Thalmann, 2000; Nash, 2004). Investigating cooperative breeding behavior in galagos may thus contribute to modeling the evolution of group-living in primates. Our expectations would be that allonursing would occur primarily with the closest kin available, and that it might have benefits which would be revealed by better growth rates among allonursed infants, compared to those that did not receive this treatment.

METHODS

Subjects

The Arizona State University Senegal bushbaby (or galago) colony (*Galago senegalensis braccatus*) housed two matrilines which descended from two founding females, E and F, who were caught in East Africa. The taxonomy and common name used here follow Groves (2001) and Nash *et al.* (1989), though this species is sometimes called the "Kenya lesser galago" (Grubb *et al.*, 2003) or the "Northern lesser bush baby" (Rowe, 1996). The matrilines were caged separately because unrelated females can be highly aggressive to each other. Across the years of the study, group sizes ranged from two to seven individuals. Each matriline was housed in a cage that was either 2.4 x 2.4 x 2.4 m high or 2.4 x 1.2 x 2.4 m high. Cages were furnished with nest

boxes, ropes, branches, and ledges. Animals were housed on a reverse light cycle (13 h light : 11 h dark) and fed daily (fresh fruit, canned primate diet, Purina monkey chow and mealworms and vitamin B supplements on alternate days) prior to the onset of the dark condition (for more details, see Nash & Flinn, 1978; Nash, 1993; Nash, 2003).

Data collection and analysis

Data are taken from focal observations of adults and 11 infants (six males, five females) in 1978-1981 as part of a larger study on infant development (Nash, 1993; Nash, 2003; Schaefer & Nash, 2007). Observations were made during the first and last three hours of darkness, which were the animals' most active times. Because observation time varied widely, from 0 to 180 min per week per infant, we binned the observation time into three-week periods. All behaviors are treated as events and rates are calculated as 'bouts/hour' within the three-week time periods. We originally distinguished between two behavior units, but later combined them for analysis as "nursing" or "allonursing" (depending on dyads): "nursing" and "probable nursing." Nursing is defined as occurring when the mother (or other) and infant are in nursing position (female in a quadrupedal position over the infant with the infant lying on its back, covered by the mother's torso, and its head at one of the sets of nipples; or with the mother lying on her side with the infant on its feet with its head at her nipples in a 'cat with kittens' position). Probable nursing is defined as occurring when the mother (or other) and infant are in nursing position but active nursing cannot be confirmed, due to absence of a clear view of the infant's behavior. We conservatively estimated that females could continue lactating for two weeks after the cessation of suckling (Izard, 1987). This could be after weaning or after the loss of an infant.

Infants were weighed approximately twice per week. The growth data were highly linear, so we estimated growth rates by performing a standardized major axis (SMA) regression, a type of model two regression, in SMATR 2.0 (Falster *et al.*, 2006).

RESULTS

From the 11 infants observed, we found six cases (55%) where there was an opportunity for allonursing to occur. Allonursing occurred in both matrilines in a total of four infants (two males, two females). For one male, this represented a single event with an older sister (see P_i, below). More prevalent allonursing also occurred in both matrilines with the remaining male and two females; each was allonursed by a maternal grandmother in 21% (n=104), 25% (n=52), and 27% (n=92) of their observed nursing bouts, respectively. To illuminate the contexts in which this occurred, we addressed each of these three infants as case studies.

Infant P_i (male)

When P_i was 18 days old, his grandmother (E) gave birth to her own infant (S_e) and he began to allonurse from E soon after. His rate of allonursing appeared to increase slightly near the time of weaning, when his rate of nursing from his mother was declining (Figure 1a). E always nursed her own infant, however, at a greater rate than she allonursed P_i (by a factor of 26 when P_i was 3-5 weeks old, and by a factor of 3 when he was 6-8 weeks old). The single allomaternal nursing event by one male infant mentioned above was when P_i's mother, I_e, allonursed S_e when S_e was 5 weeks old.

Infant T_j (female)

T_j was born one week after her grandmother finished weaning her own 18-week-old infant. Shortly after birth, T_j's rate of allonursing from her grandmother was nearly as high as her rate of nursing from her mother. Her overall rate of nursing from both her mother and grandmother tapered off over the following weeks (Figure 1b).

Infant Y_j (female)

Three days before Y_j was born, her grandmother gave birth to an infant that died on the day of birth. Y_j was allonursed by her grandmother, at a rate exceeding nursing from the mother, until she was 16 days old. At that time, Y_j's grandmother was put into a smaller cage placed within the group cage to stop her mother and grandmother from fighting over her. The grandmother was reunited with the others after four weeks and resumed allonursing Y_j. Figure 1c illustrates Y_j's rates of allonursing and nursing; the rate of nursing was highest during the time period when the grandmother was separated (resulting in an absence of allonursing due to lack of availability).

When allonursing could have occurred, but did not

Using two weeks as an estimate for how long a female could continue lactating after the cessation of suckling (Izard, 1987), we determined that there were two instances (one in each matriline) when a lactating female did not allonurse an infant in her group. Both were cases where adult females did not take advantage of the opportunity to allonurse a younger sibling. Allonursing therefore was observed in 67% of the cases (n=6) where it might have been possible.

In the first instance, the grandmother, E, gave birth to an infant at the same time as her adult daughter was nursing an infant (Figure 1a). Although both females were lactating simultaneously and the grandmother frequently allonursed her grandchild, the adult daughter did not reciprocate to the grandmother (her mother) by allonursing her own younger sibling. The adult daughter was only observed to allonurse her younger sibling once, when the infant was five weeks old, and she was observed to reject allonursing

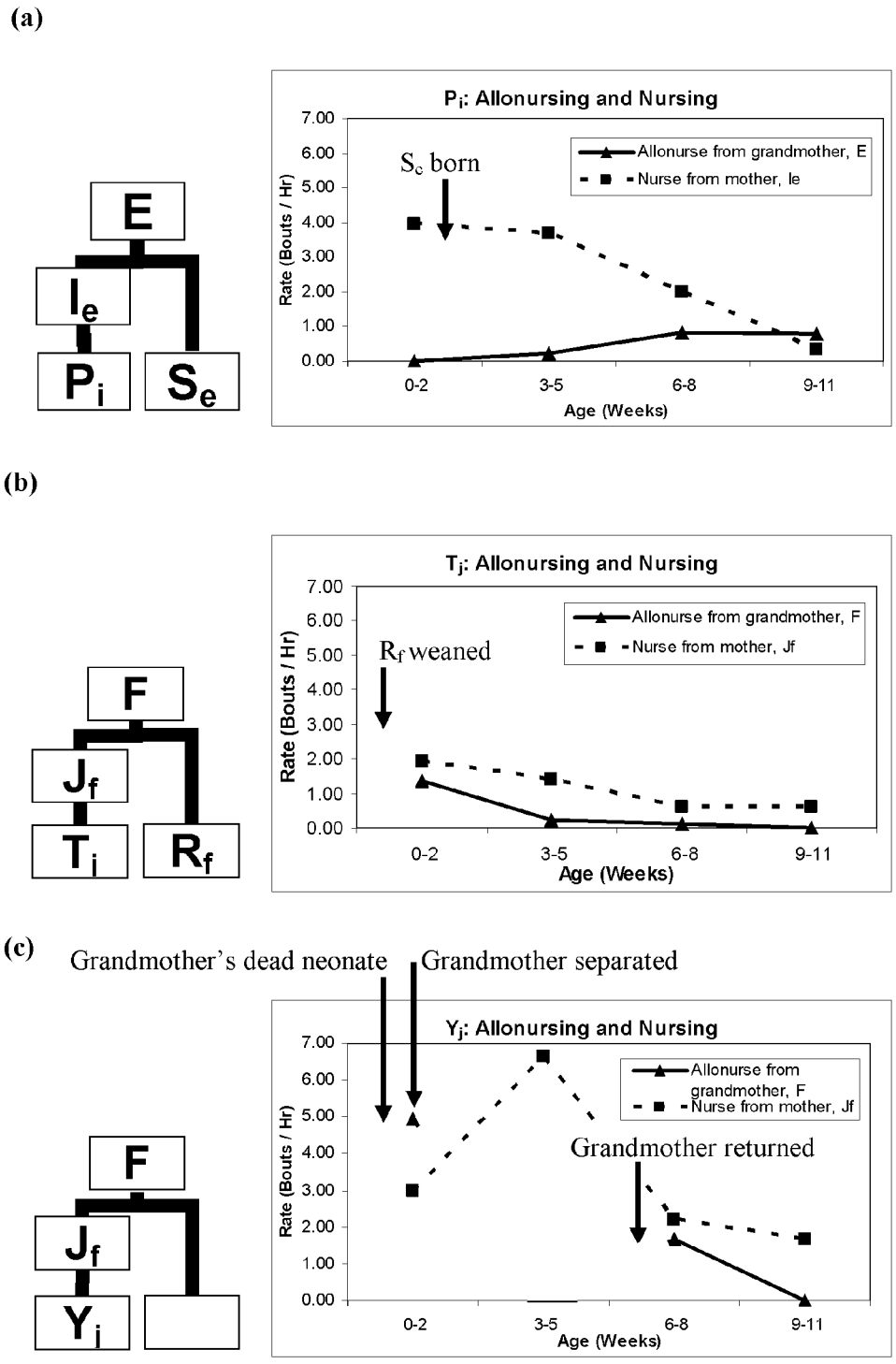

Figure 1: **(a)** A genealogy of relationships in the E matriline and a comparison of infant P_i's allonursing from his grandmother and nursing from his mother. Week zero is the week of birth. **(b)** A genealogy of relationships in the F matriline and a comparison of T_j's allonursing from her grandmother and nursing from her mother. The arrow indicates when R_f was weaned. **(c)** A genealogy of relationships in the F matriline and a comparison of Y_j's allonursing from her grandmother and nursing from her mother. Arrows indicate approximate times when the grandmother gave birth to a dead neonate (left, and indicated by the empty box in the genealogy), was separated within the group's cage (middle), and was released back into the group (right).

attempts made by the infant at six and eight weeks.

In the second instance, the grandmother, F, gave birth to an infant within two weeks of when her adult daughter, J_f, was last observed nursing an infant. Although the grandmother had frequently allonursed her grandchild (J_f's infant), her adult daughter J_f did not reciprocate to her mother (the grandmother, F) by allonursing her own younger sibling.

Growth rates

Figure 2 shows infant weight gains for the three frequently allonursed infants (referred to as 'allonursed infants') and other infants (all considered to be 'non-allonursed' infants). The RMA slopes, or g/day of weight gain, for each allonursed infant are: P_i, 1.53; T_j, 1.72; Y_j, 0.95. Other infants ranged from 1.43-1.95 g/day. Because of the small sample size of frequently allonursed infants, we did not test for statistical differences between the two groups of infants, but elected to compare the groups qualitatively. Two of the three slopes of the frequently allonursed infants are within the range of the non-allonursed infants. Y_j appears to be an outlier with unusually slow growth; however, this is likely due to the events occurring within her cage. In the first few weeks of Y_j's life, her rate of allonursing from her grandmother was *higher* than her rate of nursing from her mother. As described above, because Y_j's grandmother and mother were fighting over her and causing abrasions on her sides as they each tried to carry her by mouth (sometimes simultaneously from each side), the grandmother was removed from the cage when Y_j was 16 days old.

DISCUSSION

It is important to note that we do not know exactly when lactation stopped, and as such, it is not possible to know whether milk transfer was occurring during all of the observed allonursing bouts. The prevalence of these allonursing bouts, however, is highly suggestive of milk transfer. For three infants, over 20% of their observed nursing bouts was with their grandmother. It is also important to note that the duration of nursing was not measured, and to recall that some of the bouts included in the rates reported here were of "probable" nursing.

The absence of a difference in weight gain in two allonursed infants compared with non-allonursed infants is unexpected, as it suggests that there was no obvious benefit in terms of accelerated growth that can be associated with the allonursing. This is a captive colony, however, and we

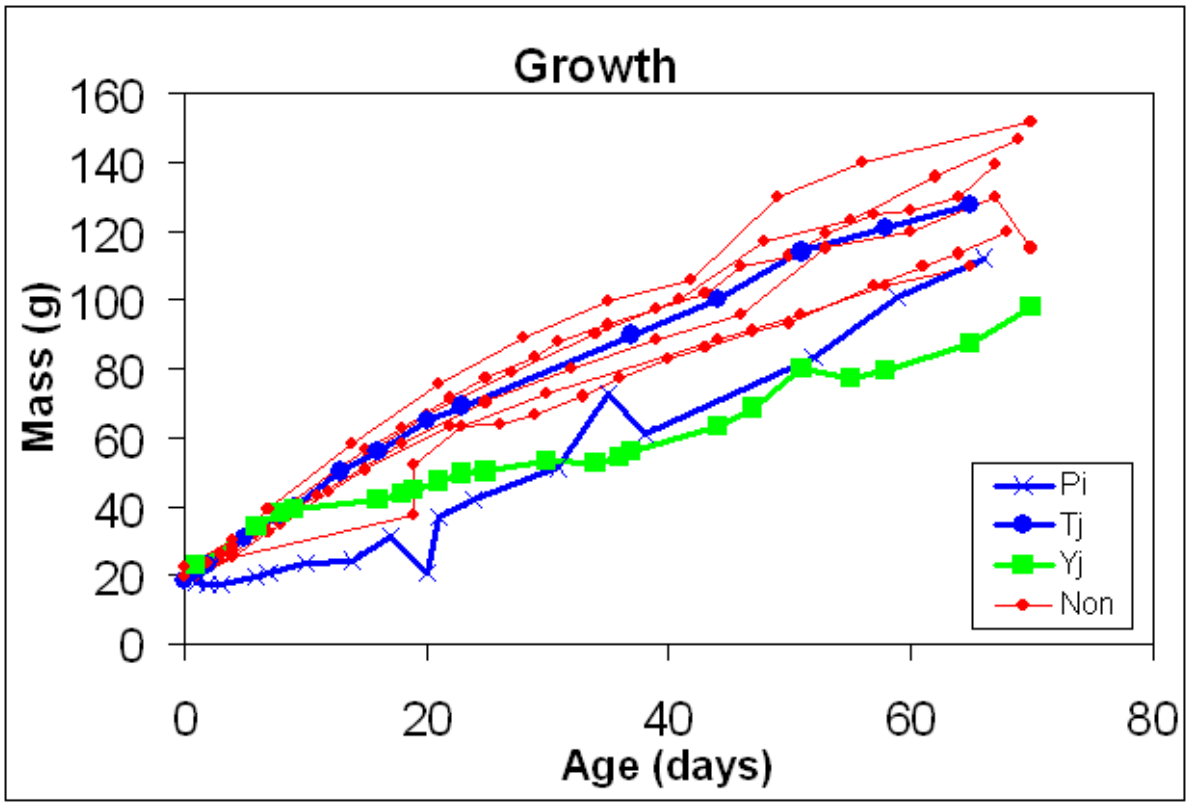

Figure 2: Weight gain for non-allonursed infants and frequently allonursed infants P_i, T_j, and Y_j for the first 70 days of life. Y_j appears to be an outlier with a qualitatively slower rate of weight gain than the other infants after her grandmother is separated when Y_j is 16 days old.

may be seeing a 'ceiling effect' where all infants are usually sufficiently well-fed to grow at a maximal rate. In the case of Y_j's rate of weight gain, which seemed low, it slowed at the time when she may have been stressed due to the rough treatment she received as her mother and grandmother competed over access to her. Given that Y_j's slow weight gain could be explained by the events occurring within her cage, we conclude that our qualitative analyses of the growth rates do not suggest that there are likely to be differences in growth rate between allonursed and non-allonursed infants due to the nursing *alone*. Alternatively, Y_j's slowed weight gain at the time when the grandmother was separated might be because she was benefiting from additional milk from her grandmother which became unavailable when her grandmother was removed from the group. There was a slight upward inflection in her growth at about the time the grandmother was returned (in Y_j's 6^{th} week of age). Full interpretation of the costs and benefits of allonursing is also limited, however, because the composition of milk for this species is unknown. Even for the closely related *G. moholi*, data are limited to one sample from one female (Tilden & Oftedal, 1997).

Our data also suggest that there is an intriguing contrast between the allonursing behavior of grandmothers and adult daughters. While grandmothers were observed to allonurse frequently, adult daughters rarely allonursed younger siblings. This suggests that grandmothering in galagos may be a reproductive strategy that enables older females, whose reproductive value is declining, to increase their reproductive success. An alternative, nonadaptive explanation, however, might be that there is a 'Kindchenschema' (Lorenz, 1943) that attracts females to care for infants and that the threshold for activating that innate releasing mechanism is lower in the grandmother than the mother. Since both females will both tolerate each other close to the infant, an 'unintended consequence' of these proximate mechanisms might be conflict over an infant. Our lack of information about the regularity with which two females co-nest in the wild, however, limits our ability to discriminate between these hypotheses.

While our results suggest that age and, possibly, reproductive value are important factors in determining whether a female will allonurse her kin, these results are preliminary and we still do not know how other factors may influence a female's decision regarding allonursing. Potentially important factors include the actual frequency of opportunities where lactating females share a range and a nest for young, the degree of relatedness of the infant (e.g., potential sibling rivals), the female's condition, the infant's condition, and the level of agonism and food competition between the co-nesting females. It also would be useful to know how infants discriminate between the mother and familiar females, or even if they do, as experimental work on this issue is ambiguous (Nash, 1987). Each of these factors merits future research.

Although captive and wild behavior and life history may differ, our work suggests that *G. senegalensis* has the potential to breed cooperatively in the wild. More fieldwork is needed to determine whether or not they actually do so. This species of galago is greatly neglected in terms of modern field study and no details of its social behavior in the wild are quantified (Nash & Whitten, 1989; Bearder *et al.*, 2003; Off *et al.*, 2008), in contrast to *G. moholi*, which has been the subject of detailed fieldwork (Bearder & Martin, 1980; Pullen, 2000; Pullen *et al.*, 2000; Nekaris & Bearder, 2007). Our observations also suggest that captivity not only may increase the potential for cooperative breeding, but also the possible costs, if infants become objects of contention between females. More field observations also would enable cross-species comparisons to investigate why some galagos appear to alloparent while others do not. Studies employing the 'within nest' video technology that has been applied to mouse lemurs would be especially useful (Eberle & Kappeler, 2006). Future work examining the impacts of ecological variation on cooperative breeding behavior in galagos would likely to be an informative comparison to similar data on the hypometabolic mouse lemur species (Radespiel, 2006). Additional findings of cooperative breeding in wild galagos also would support the idea that alloparenting may have occurred in ancestral, nongregarious primates. Unless the habitats and populations of all galago species are protected, however, such comparative work will never be possible. The various galago species are often neglected in conservation plans for an area (Nekaris & Bearder, 2007). Research on the behavior and ecology of this species should receive continued support, as it is now well established that longitudinal research can be an important adjunct to conservation efforts (Wrangham & Ross, 2008).

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Mother and Infant Galago senegalensis
Photograph by Leanne T. Nash